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Frisvad, J.C.

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A critical review of producers of small lactone mycotoxins: patulin, penicillic acid and moniliformin

J.C. Frisvad

Department of Biotechnology and Biomedicine, Technical University of Denmark, Søltofts Plads Building 221, 2800 Kgs. Lyngby, Denmark; jcf@bio.dtu.dk

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REVIEW ARTICLE

Abstract

A very large number of filamentous fungi has been reported to produce the small lactone mycotoxins patulin, penicillic acid and moniliformin. Among the 167 reported fungal producers of patulin, only production by 29 species could be confirmed. Patulin is produced by 3 *Aspergillus* species, 3 *Paecilomyces* species, 22 *Penicillium* species from 7 sections of *Penicillium*, and one *Xylaria* species. Among 101 reported producers of penicillic acid, 48 species could produce this mycotoxin. Penicillic acid is produced by 23 species in section *Aspergillus* subgenus *Circumdati* section *Circumdati,* by *Malbranchea aurantiaca* and by 24 *Penicillium* species from 9 sections in *Penicillium* and one species that does not actually belong to *Penicillium* (*P. megasporum*). Among 40 reported producers of moniliformin, five species have been regarded as doubtful producers of this mycotoxin or are now regarded as taxonomic synonyms. Moniliformin is produced by 34 *Fusarium* species and one *Penicillium* species. All the accepted producers of patulin, penicillic acid and moniliformin were revised according to the new one fungus – one name nomenclatural system, and the most recently accepted taxonomy of the species.

Keywords: patulin, penicillic acid, moniliformin, terrestric acid, *Penicillium, Aspergillus, Fusarium*

1. Introduction

Small toxic lactones, especially patulin, penicillic acid and moniliformin are recognised mycotoxins (Bemi, 2004; Ciegler *et al.*, 1971; Gaucher, 1979; McKinley and Carlton, 1991; Moake *et al.*, 2005; Puel *et al.*, 2010; Schütt *et al.*, 1998; Scott, 1974; Wilson, 1976), even though only patulin is under regulation (EC, 2003). They share some properties apart from being toxic and having some structural similarities. They are all polar, acidic, secondary metabolites often produced in large amounts in foods and feeds (Ciegler *et al.*, 1971), even though they differ in the niches their producers occupy: patulin is often associated with fruits and penicillic acid and moniliformin with cereals. Patulin and penicillic acid were early on recognised as effective antibiotics (Chain *et al.*, 1942; Florey *et al.*, 1949; Korzybski *et al.*, 1967; Oxford *et al.*, 1942; Singh, 1967), and have later been show also to inhibit quorum sensing in bacteria (Rasmussen *et al.*, 2005). Patulin and penicillic acid also share a specific reaction with the sulfhydryl-containing amino acids cysteine and gluthatione (Larsen and Olson, 1992; Morgavi *et al.*, 2003). While this may help inactivating these mycotoxins in foods containing cysteine and gluthatione, those data indicate that part of the toxic effect of the small lactones is the binding of S-containing amino acids in proteins.

Apart from being an effective antibiotic, patulin can also produce petit mutants in *Saccharomyces cerevisiae* (Mayer and Legator, 1969). Patulin can act as a phytotoxin (Ellis *et al.*, 1977; Florey *et al.*, 1949; Ismail and Papenbrock, 2015; Korzybski *et al.*, 1967; Scott, 1974) and is active against pathogenic fungi (Gilliver, 1946; Herrick, 1945; Sanders, 1946). Patulin was initially suggested for treatment of common cold (Birkinshaw *et al.*, 1943; Gye, 1943), as it is anti-viral (Detroy and Still, 1975) in addition to being antibacterial, but the trials on humans were quickly dropped because of the toxicity of patulin.

Patulin has been reported to be acutely toxic (Ciegler, 1977; Devaraj *et al.*, 1986; Drusch and Ragab, 2003; Engel and Teuber, 1984; Escoula *et al.*, 1977; Fung and Clark, 2004; Hayes *et al.*, 1979; Hopkins, 1993; McKinley and Carlton, 1980a,b; McKinley *et al.*, 1982; Wouters and Speijers, 1996), teratogenic (Ciegler *et al.*, 1976; Vesely and Vesela, 1991), cardiotoxic (Vesely and Vesela, 1991), it influences the colonic epithelial permeability (Maidana *et al.*, 2016; Mohan *et al.*, 2012), and it is immunotoxic (Bourdiol *et al.*, 1990; Escoula *et al.*, 1988; Paucod *et al.*, 1990; Sharma, 1993). Patulin is first of all found in pomaceous foods like apples and pears, but also in other fruits (Beretta *et al.*, 2000; Jackson and Dombrinck-Kurtzman, 2006; Yang *et al.*, 2014).

Penicillic acid was first reported by Alsberg and Black (1913) in an examination of fungal growth in maize and potential fungal involvement in pellagra. Its structure was elucidated by Birkinshaw *et al.* (1936) and its antibacterial effect against Gram positive and Gram negative bacteria was first reported by Oxford in 1942, Oxford *et al.* in 1942 and Geiger and Conn in 1945, as reviewed by Korzybski *et al.* (1967). Later the antibiotic effect of penicillic acid has also been reported by Ezzat *et al.* (2007). Penicillic acid is also very inhibitory towards *Phytophthora* species (Kang and Kim, 2004). Furthermore, penicillic acid is phytotoxic (Ismaiel and Papenbrock, 2015).

Penicillic acid has been shown to be acutely toxic to poultry, mice, rats and rabbits (Cole and Cox, 1981). Furthermore, it dilates blood vessels and possesses antidiuretic properties (Murnaghan, 1946). Penicillic acid has been involved in broiler chicken mycotoxicosis (Ghadevaru, 2013; Samadha and Balachandran, 2008; Sarmadha *et al.*, 2008) but gingerol has been shown to alleviate the toxic effects of penicillic acid (Pazhavinel *et al.*, 2015). Penicillic acid is cytotoxic (Grabsch *et al.*, 2006), hepatotoxic (Chan and Hayes, 1981), and has been claimed to be carcinogenic and cardiotoxic (Dickens and Jones, 1961, 1963, 1965; Vesely and Vesela, 1991), and a sodium, potassium and calcium channel blocker in frog hearts (Pandiyan *et al.*, 1990). It is also toxic to rat alveolar macrophages (Sorenson and Simpson, 1986).

Ochratoxin A and penicillic acid show synergistic toxicity on bovine macrophage cell lines (Oh *et al.*, 2015), in chickens (Kubena *et al.*, 1984; Micco *et al.*, 1989), in the corn ear worm and the fall armyworm (Dowd, 1989). The two toxins together also increase degeneration in kidney proximal tubules (Klarić *et al.*, 2013; Stoev, 2013; Stoev and Denev, 2013). The synergistic worm toxicity of penicilllic acid and ochratoxin A is interesting as the fungi producing these combinations of toxins are often growing in corn and other cereals (Lund and Frisvad, 1994; Visagie *et al.*, 2014a). Other studies have only shown an additive toxic effect on porcine lymphocytes of ochratoxin A and penicillic acid (Bernhoft *et al.*, 2004; Stoev *et al.*, 1999). These two mycotoxins are often co-occurring as *Aspergillus* from section *Circumdati* produce penicillic acid and ochratoxin simultaneously in most species from that section (Visagie *et al.*, 2014a). Furthermore, species from *Penicillium* section *Fasciculata* series *Viridicata* and *Verrucosa* co-occur in cereals (Lund and Frisvad, 1995), and thus penicillic acid and ochratoxin A are also both found often in contaminated cereals.

It has been suggested that ochratoxin A and penicillic acid may both be involved in Balkan Endemic Nephropathy (Stoev, 2017; Stoev *et al.*, 2001). *Penicillium polonicum* and *Penicillium aurantiogriseum,* both producing penicillic acid, verrucosidin and nephrotoxic glycopeptides, are often found in the Balkan countries, but *Penicillium verrucosum*, the main ochratoxin A producing *Penicillium* species in cereals, is found less often (MacGeorge and Mantle, 1990; Mantle, 1994; Mantle *et al.*, 2010; Miljkovic *et al.*, 2003; Stoev *et al.*, 2010; Yeulet *et al.*, 1988). Penicillic acid is mostly found in cereals (Bokhari and Flannigan, 1996; Chełkowski and Golinski, 1983; Chełkowski *et al.*, 1983, 1987; Kurtzman and Ciegler, 1970; Szebiotko *et al.*, 1981; Tangni and Pussemier, 2007) and some other products like cassava (Wareing *et al.*, 2001).

Terrestric acid is rather closely related to penicillic acid, and is produced by *P. aurantiogriseum, Penicillium crustosum* (= *Penicillium terrestre*), *Penicillium hirsutum, Penicillium hordei, Penicillium radicicola, Penicillium tricolor, Penicillium tulipae, Penicillium venetum* and *Magnaporte grisea* = *Pyricularia oryzae* (Birkinshaw and Raistrick, 1936; Frisvad and Samson, 2004; Frisvad *et al.*, 1994, 2004; Lund and Frisvad, 1994; Overy and Frisvad, 2003; Overy *et al.*, 2005; Sonjak *et al.*, 2005; Yu *et al.*, 2010). Production of terrestric acid by *Penicillium griseoroseum* (Da Silva *et al.*, 2013), and *Penicillium viridicatum* (Birkinshaw and Samant, 1960) could not be confirmed (Frisvad and Samson, 2004), other metabolites produced by these organisms indicate they were in fact *P. crustosum* (Frisvad *et al.*, 2014). Terrestric acid has also been reported from *P. hirsutum* var. *albocoremium* (Frisvad and Filtenborg, 1989), but this taxon was later subdivided in *Penicillium albocoremium*, *P. radicicola and P. tulipae*. Only the last two species produce terrestric acid (Overy and Frisvad, 2003; Overy *et al.*, 2005). This small acidic lactone is also phytotoxic (Nukina, 1988) and cardiotoxic (Giarman, 1948, 1949), thus resembling penicillic acid in some of its bioactivities. *P. aurantiogriseum*, *P. radicicola* and *P. tulipae* can produce both penicillic acid and terrestric acid (Frisvad *et al.*, 2004; Overy and Frisvad, 2003; Overy *et al.*, 2005).

Like penicillic acid, moniliformin has also been found in cereals and other plant products (Herrare *et al.*, 2017; Kovalsky *et al.*, 2016; Neme and Mohammed, 2017; Uhlig *et al.*, 2004). An important fact is that while moniliformin is mostly produced by important field-fungi, such as *Fusarium* spp., penicillic acid is produced by storage fungi only. Moniliformin has not been reported as an antibiotic or quorum sensing inhibitor in bacteria (Bacon *et al.*, 2017), but moniliformin is acutely toxic to poultry (Burmeister *et al.*, 1979; Cole *et al.*, 1973; Sharma *et al.*, 2008) and rats (Chen *et al.*, 1990; Jonsson *et al.*, 2013, 2015; Thiel, 1978), in the latter study indicating a severe impact on the immune system. It inhibits several enzymes important in metabolism (Burka *et al.*, 1982). It is cardiotoxic and effects mammalian smooth muscle (Kamyar *et al.*, 2006; Peltonen *et al.*, 2010). Moniliformin is also phytotoxic and has plant growth-regulating properties (Cole *et al.*, 1973).

There is one example of co-production of penicillic acid and patulin by *Penicillium roqueforti* (Olivigni and Bullerman, 1977, 1978), but the producing organism was reidentified to *Penicillium carneum* later (Boysen *et al.*, 1996; Frisvad and Samson, 2004; Frisvad *et al.*, 2004). *Penicillium melanoconidium* has been reported to produce moniliformin and penicillic acid (Hallas-Møller *et al.*, 2016), but no species has been reported to produce patulin and moniliformin concomitantly.

It was the aim of this review to revise the lists of producers of patulin, penicillic acid and moniliformin according to the most recent taxonomic treatments of the genera *Aspergillus* (Chen *et al.*, 2016a,b, 2017; Frisvad, 2015; Frisvad and Larsen, 2015; Hubka *et al.*, 2015, 2016; Jurjevics *et al.*, 2015; Kocsubé *et al.*, 2016; Samson *et al.*, 2011a,b, 2014, 2017; Sklenář *et al.*, 2017; Varga *et al.*, 2007a,b, 2011a,b; Visagie *et al.*, 2014a, 2017), *Penicillium* (Frisvad and Samson, 2004; Houbraken *et al.*, 2016; Visagie *et al.*, 2014b) and *Fusarium* (Aoki *et al.*, 2014; Burgess, 2014; Gerlach and Nirenberg, 1982; Lesley and Summerell, 2016; Nelson *et al.*, 1983), as correct species-mycotoxin relations are important for prevention of mycotoxin formation in foods, feeds and biotechnological products.

2. Criteria for accepting a species as a producer of one or more small toxic lactones

Confirmation of mycotoxin production by a species of a filamentous fungus requires that both the fungus and the mycotoxin are correctly identified. Furthermore, it should be verified that the fungus examined is a pure culture. Also the fungal strain producing the mycotoxins should be available to the scientific community. In several cases the producing fungi were never accessioned in a culture collection, so the experiments could not be repeated and the identity of the fungal strain could not be verified or validated. If the mycotoxinogenic isolate was identified using a polyphasic approach, using a combination of morphological, physiological, chemical, and molecular features, the identifications are often correct. Molecular identification should be based on sequences of several genes, because ITS sequences are not always sufficient for correct identification at the species level (Raja *et al.*, 2017; Seifert *et al.*, 2007). Several independent reports of production of a particular mycotoxin by a particular fungal species adds to the credulity of a species-mycotoxin connection (Frisvad, 1989; Frisvad and Samson, 2004). Often production of a particular secondary metabolite is taxonomically restricted to rather few, often phylogenetically related species, so unexpected mycotoxin formation from phylogenetically unrelated species to known producers should be confirmed with special care. It should be noted that some groups of species have been revised several times, so a name that was valid earlier now may just be a synonym or a rejected name. Furthermore, the one fungus – one name system introduced in 2011 has caused a lot of changes. For example species earlier called *Eurotium*, *Neosartorya*, *Emericella* are now all called *Aspergillus* (Samson *et al.*, 2014) and *Fusarium* is the preferred name for species formerly allocated to *Gibberella* (Geiser *et al.*, 2013). It also adds to the credulity of the reported specific mycotoxin production, if the toxin has been detected in a large number of isolates in the species examined.

It should also be documented that the growth medium used for mycotoxin production does not contain the mycotoxin already. Often secondary metabolites are accumulated, so repeated reporting of trace amounts of mycotoxins on media otherwise suited for production may indicate that the mycotoxin was already present in the growth medium. This is most important for media based on cereals, as these can contain trace amounts of mycotoxins if field or storage fungi have grown in such substrates. It is in general recommended to analyse control samples for mycotoxins and use chemically defined media in a confirmation of mycotoxin production, if unexpected results have been obtained using plant based media.

Chemical analysis, for example using HPLC methods for separation and combined with sensitive detection methods will also inherently carry the risk of carry over of mycotoxins, so here proper controls are also needed. Chromatographic and spectrometric verification of the identity of the mycotoxin is needed to guard against false positives. If the retention times in several chromatographic systems is equal to the retention time of an authentic chemical standard, this is valuable confirmation of identity, but on top of that high resolution mass spectra (MS) and/or UV spectra, as compared to an authentic standard are necessary to confirm identity. It is recommended to have at least 3 different independent confirmations of identity, and one of them should preferably be high resolution mass spectrometry (identical mass ions and relevant adducts as compared to a standard) and even the same mass fragmentation pattern as an authentic standard. Occasionally chemical identity is confirmed by nuclear magnetic resonance (NMR) characterisation, circular dichroism (CD) spectra, fourier transform infrared (FTIR) spectra, etc., especially the first time a secondary metabolite is structure elucidated and isolated from a particular species. NMR, CD and FTIR can also be used for a very solid confirmation of identity. Other types of data, for example detection of biosynthetic precursors, and discovery of the gene cluster or part of it for the particular mycotoxin under scrutiny adds further data to support a mycotoxin-fungal species connection. The criteria for accepting a fungus as a producer of patulin, penicillic acid or moniliformin include the following: production has been reported several times and in several different strains (more than one time and from different research groups), fungal identification has been documented, the fungal producing strains are available for the scientific community, and at least three chromatographic and spectrometric kinds of confirmatory data have been provided. If, in addition, parts of the gene cluster for the mycotoxins have been found, NMR data for the mycotoxin have been made available, or the biosynthesis has been confirmed, for example by detecting biosynthetic precursors, the documentation for such relationships is of course even stronger.

3. Patulin and producing organisms

The biosynthesis of patulin, starting from 6-methyl salicylic acid is well known (Barad *et al.*, 2016c; Birch *et al.*, 1955; Bu'Lock and Ryan 1958; Dimroth *et al.*, 1976; Forrester and Gaucher, 1972a,b; Priest, 1989; Puel *et al.*, 2010; Scott *et al.*, 1971, 1972; Sekiguchi, 1983; Sekiguchi and Gaucher, 1978; Tanenbaum and Bassett, 1959), and the gene cluster for patulin has been found in different producing filamentous fungi (Ballester *et al.*, 2015; Barad *et al.*, 2016c; Dombrink-Kurtzman, 2007; Li *et al.*, 2015; Nielsen *et al.*, 2017; Puel *et al.*, 2010; Snini *et al.*, 2014; Tannous *et al.*, 2014). The role of patulin itself in the fruit infection process has not been fully elucidated (Barad *et al.*, 2016a,b), but it has been suggested that accumulation of both gluconic acid and patulin (Barad *et al.*, 2012, 2014, 2016a; Snini *et al.*, 2015) will make *Penicillium expansum* a more aggressive post-harvest pathogen. However, patulin may also be important for *P.expansum* itself in the competition with other microorganisms thriving in the fruit. It should be noted that the two other apple pathogenic Penicillia, *Penicillium solitum* and *P. crustosum*, do not produce patulin (Frisvad and Samson, 2004; Sanderson and Spotts, 1995), questioning the importance of patulin in the infection process.

The main end-product is patulin itself, but other related toxins are known, such as neopatulin, isopatulin, desoxypatulinic acid, ascladiol, longianone and pintulin (Appell *et al.*, 2009; Bennett *et al.*, 1990, 1991; Ghisalberti *et al.*, 2000; Lykakis *et al.*, 2009; Mikami *et al.*, 1996; Scott *et al.*, 1972; Sekiguchi *et al.*, 1979).

Many strains producing patulin have been genome sequenced, including *P. expansum* (Ballester *et al.*, 2015; Barad *et al.*, 2016c; Julca *et al.*, 2015; Yin *et al.*, 2017; Yu *et al.*, 2014), *P. griseofulvum* (Banani *et al.*, 2016), *Penicillium antarcticum*, *P. carneum*, *Penicillium paneum*, and *Penicillium vulpinum* (Nielsen *et al.*, 2017). A comparison of the gene clusters for patulin production in the different species shows they are quite similar, and that *P. roqueforti* has part of the gene cluster needed to produce patulin, but lacks essential genes, making it unable to produce patulin (Nielsen *et al.*, 2017).

Patulin has been reported from 166 different species, varieties and chemotypes (Table 1), but the documentation for some of all these producers is occasionally doubtful. In many of the publications, the original producers reported are not available to the scientific community. For example, in the papers by Steiman *et al.* (1989), Okeke *et al.* (1993), and Oh *et al.* (1998), accession numbers of the fungi examined are not available, and thus it is not possible to verify the identity of the producers. In the paper by Okeke *et al.* (1993) some very efficient producers of patulin are reported, often known producers of patulin, such as *P. expansum*, while most of the trace producers of patulin are fungi not expected to produce patulin, such as *Trichothecium roseum*. It has been a general experience that when a fungus can produce patulin, it will always accumulate large amounts of the toxin, never a small trace of a toxin (Frisvad, personal observations). It is tempting to speculate that the detection of patulin in unexpected species was caused by carry over in the HPLC chromatographic system or because of contamination with efficient patulin producers. Patulin has been found in sections *Canescentia*, *Formosana, Gladioli, Osmophila, Penicillium, Ramosa* and *Robsamsonia* in *Penicillium,* but only in section *Clavati* in *Aspergillus*.

Patulin has the formula $C_7H_6O_4$, and a molecular mass of 154, and a monoisotopic mass of 154.026. Searching in the Microbial secondary metabolite database AntiBase with approximately 40,000 natural products, 95 secondary metabolites have the molecular mass of 154, while 13 fungal secondary metabolites had a monoisotopic mass of 154.026, including members of the patulin biosynthetic pathway patulin, isopatulin, neopatulin, gentisic acid, longianone and (-)-phyllostine. However, other secondary metabolites, such as terreic acid and terremutin also have the monoisotopic mass of 154.026. This may be the reason *Aspergillus terreus* was reported to produce patulin (Draughon and Ayers, 1980; El-Shanawany *et al.*, 2005; Escoula, 1974; Girisham and Reddy, 1986a,b; Giridhar and Reddy, 1998; Kent and Heatley, 1945; Reddy and Reddy, 1984, 1988), while it was probably terreic acid that was detected. Given several references on patulin production by *A. terreus*, it cannot be excluded that this species, or one of the closely related species, can produce it. Obviously for such small molecules, mass spectrometric (MS) verification is of value, but has to be combined with other data, such as an UV spectrum identical to that of patulin and retention time verification,

Table 1. Filamentous fungi claimed to produce patulin (also called clavacin, clavatin, claviformin, expansin and penicidin).

Fungal species	References	Synonymised species
Acremonium implicatum	Ismaiel *et al.*, 2016	
Acremonium persicinum	Okeke *et al.*, 1993	
Acremonium sclerotigenum	Okeke *et al.*, 1993	
Acremonium zeae	Steiman *et al.*, 1989	
Alternaria alternata	Drusch and Ragab, 2003; Leidou *et al.*, 2001; Steiman *et al.*, 1989	
Alternaria papaveris	Steiman *et al.*, 1989	
Alternaria tenuissima	Okeke *et al.*, 1993	
Ascochyta imperfecta	Steiman *et al.*, 1989	
Aspergillus amstelodami	Steiman *et al.*, 1989	
Aspergillus candidus	Frank, 1977	
Aspergillus clavatus	Bergel *et al.*, 1943, 1944; Diaz and Flannigan, 1997; Escoula, 1974; Lopez-Varga *et al.*, 2007; Paterson, 2004 (IDH gene); Umezawa *et al.*, 1947; Wiesner, 1942	
Aspergillus echinulatus	Steiman *et al.*, 1989	
Aspergillus flavus	Luque *et al.*, 2011	
Aspergillus fumigatus	Steiman *et al.*, 1989	
Aspergillus giganteus	Florey *et al.*, 1944; Okeke *et al.*, 1993; Paterson, 2004 (IDH gene); Varga *et al.*, 2007a	
Aspergillus longivesica	Varga *et al.*, 2007a	
Aspergillus manginii	Steiman *et al.*, 1989	
Aspergillus ochraceus	Abu-Seidah, 2003	
Aspergillus oryzae	Chunmei *et al.*, 2013; Luque *et al.*, 2011	
Aspergillus parasiticus	Steiman *et al.*, 1989	
Aspergillus petrakii	Okeke *et al.*, 1993	
Aspergillus repens	Steiman *et al.*, 1989	
Aspergillus sydowii	Chunmei *et al.*, 2013	
Aspergillus tamarii	Luque *et al.*, 2011	
Aspergillus terreus	Couch and Gaucher, 2004 (MSA gene); El-Shanawany *et al.*, 2005; Escoula, 1974; Draughon and Ayers; 1980; Giridhar and Reddy, 1998; Girisham and Reddy, 1986a;b; Kent and Heatley, 1945; Paterson, 2004 (IDH gene); Reddy and Reddy, 1984, 1988	
Aspergillus variecolor	Steiman *et al.*, 1989	
Aspergillus versicolor	Steiman *et al.*, 1989	
Aureobasidium pullulans var. *pullulans*	Steiman *et al.*, 1989	
'Basidio 2'	Steiman *et al.*, 1989	
Botrytis allii	Steiman *et al.*, 1989	
Byssochlamys fulva	Escoula, 1974; Paterson, 2004 (IDH gene); Sant'Ana *et al.*, 2010; rejected by Puel *et al.*, 2007	see *Paecilomyces fulvus*
Byssochlamys nivea	Escoula, 1974; Kis *et al.*, 1969; Paterson, 2004 (IDH gene); Sant'Ana *et al.*, 2010; Scurti *et al.*, 1973	see *Paecilomyces niveus*
Calcarisporium arbuscula	Okeke *et al.*, 1993; Steiman *et al.*, 1989	
Chaetomium atrobrunneum	Okeke *et al.*, 1993	
Chondrostereum purpureum	Okeke *et al.*, 1993	
Chrysosporium pannorum	Steiman *et al.*, 1989	now *Geomyces pannorum*
Cladobotryum varium	Steiman *et al.*, 1989	
Cladobotryum verticillatum	Steiman *et al.*, 1989	
Cladorrhinium sp.	Okeke *et al.*, 1993; Steiman *et al.*, 1989	
Colletotrichum musae	Steiman *et al.*, 1989	
Coniothyrium sp.	Okeke *et al.*, 1993	
Cunninghamella bainieri	Steiman *et al.*, 1989	
Curvularia lunata	Steiman *et al.*, 1989	
Cylindrocarpon cylindroides	Okeke *et al.*, 1993	
Cylindrocarpon ianthotele	Okeke *et al.*, 1993	
Cylindrocarpon olidum	Okeke *et al.*, 1993	

Table 1. Continued.

Fungal species	References	Synonymised species
Dichotomomyces cejpii	Okeke *et al.*, 1993	
Emericella quadrilineata	Luque *et al.*, 2011	
Emericella rugulosa	Luque *et al.*, 2011	
Emericella variecolor	Luque *et al.*, 2011	
Eupenicillium brefeldianum	Okeke *et al.*, 1993; Steiman *et al.*, 1989	
Eupenicillium javanicum	Okeke *et al.*, 1993	
Eupenicillium sp. 1	Okeke *et al.*, 1993	
Eupenicillium sp. 2	Okeke *et al.*, 1993	
Fusarium culmorum	Steiman *et al.*, 1989	
Fusarium proliferatum var. *proliferatum*	Steiman *et al.*, 1989	
Fusarium sp.	Xie *et al.*, 2011	
Gymnoascus sp.	Karow and Forster, 1944; Kuehn, 1958	
Gymnoascus reesii	Okeke *et al.*, 1993; Steiman *et al.*, 1989	
Mortierella bainieri	Steiman *et al.*, 1989	
Mucor hiemalis	Steiman *et al.*, 1989	
Mucor racemosus var. *globosus*	Steiman *et al.*, 1989	
Oidiodendron echinulatum	Steiman *et al.*, 1989	
Oidiodendron tenuissimum	Steiman *et al.*, 1989	
Paecilomyces lilacinus	Okeke *et al.*, 1993; Steiman *et al.*, 1989	
Paecilomyces variotii	Escoula, 1975; Paterson, 2004 (IDH gene)	
Paecilomyces fulvus	renamed here from *Byssochlamys fulva*	
Paecilomyces niveus	renamed here from *Byssochlamys nivea*	
Paecilomyces saturatus	Samson *et al.*, 2009	
Penicillium antarcticum	Vansteelandt *et al.*, 2012	
Penicillium asperosporum	Moslem *et al.*, 2011	
Penicillium aurantiogriseum	Luque *et al.*, 2011; Moslem *et al.*, 2010; Oh *et al.*, 1998; Okeke *et al.*, 1993; Paterson, 2004 (IDH gene); Paterson *et al.*, 2003; Steiman *et al.*, 1989	
Penicillium brevicompactum	Paterson, 2004 (IDH gene); Paterson *et al.*, 2003	
Penicillium camemberti	Luque *et al.*, 2011	
Penicillium canescens	Steiman *et al.*, 1989	
Penicillium carneum	Boysen *et al.*, 1996; Dombrinck-Kurtzman, 2007; Nielsen *et al.*, 2006	
Penicillium chrysogenum	Chunmei *et al.*, 2013; Leistner and Pitt, 1977; Oh *et al.*, 1998; Steiman *et al.*, 1989	
Penicillium citreonigrum	Steiman *et al.*, 1989	
Penicillium citrinum	El-Samawaty *et al.*, 2013; Frank, 1977; Oh *et al.*, 1998	
Penicillium claviforme	Afiyatullov *et al.*, 2015; Bergel *et al.*, 1943; Borkowska Opacka and Escoula, 1977; Chain *et al.*, 1942; Frisvad and Filtenborg, 1983	see ***P. vulpinum***
Penicillium clavigerum	Dombrinck-Kurtzman, 2007; Dombrink-Kurtzman and Blackburn, 2005; Svendsen and Frisvad, 1994	
Penicillium commune	Luque *et al.*, 2011; Oh *et al.*, 1998	
Penicillium compactum	Houbraken *et al.*, 2016	
Penicillium concentricum	Dombrinck-Kurtzman, 2007; Frisvad and Samson, 2004; Frisvad *et al.*, 2004; Leistner and Eckardt, 1979	
Penicillium concentricum II	Frisvad and Filtenborg, 1983; Houbraken *et al.*, 2016	see ***P. coprobium***
Penicillium coprobium	Frisvad and Filtenborg, 1989; Frisvad and Samson, 2004; Frisvad *et al.*, 2004; Dombrink-Kurtzman and Blackburn, 2005; Houbraken *et al.*, 2016	
Penicillium corylophilum	Paterson, 2004 (IDH gene); Vismer *et al.*, 1996	
Penicillium crustosum	Northolt *et al.*, 1978; Yun *et al.*, 2006	
Penicillium cyaneofulvum	Berestetskii *et al.*, 1974	
Penicillium cyaneum	Okeke *et al.*, 1993	

Table 1. Continued.

Fungal species	References	Synonymised species
Penicillium cyclopium	Efimenko and Yakimov, 1960; Frank, 1972; 1977; Leistner and Pitt, 1977	
Penicillium dipodomyicola	Dombrinck-Kurtzman, 2007; Frisvad and Samson, 2004; Frisvad *et al.*, 1987, 2004; Houbraken *et al.*, 2016; Luque *et al.*, 2011	
Penicillium dipodomyis	Koteswara Rao *et al.*, 2011	
Penicillium divergens	Barta and Mecir, 1948,	see ***P. glandicola***
Penicillium diversum	Okeke *et al.*, 1993	
Penicillium duclaucxii	Okeke *et al.*, 1993	
Penicillium echinulatum	Okeke *et al.*, 1993	
Penicillium equinum	Burton, 1949; Burton and Pausacker, 1947	see ***P. expansum***
Penicillium expansum	Luijk, 1938; Andersen *et al.*, 2004; Anslow *et al.*, 1943; Borkowska Opacka and Escoula, 1977; Casquete *et al.*, 2017; Chunmei *et al.*, 2013; Dombrinck-Kurtzman, 2007; Dombrink-Kurtzman and Blackburn, 2005; El-Samawaty *et al.*, 2013; Frisvad and Filtenborg, 1983; Harwig *et al.*, 1973; Larsen *et al.*, 1998; Okeke *et al.*, 1993; Paster *et al.*, 1995; Paterson, 2004 (IDH gene); Paterson *et al.*, 2003; Sommer *et al.*, 1974; Steiman *et al.*, 1989; Welke *et al.*, 2011	
Penicillium fellutanum	Vismer *et al.*, 1996	
Penicillium funiculosum	Steiman *et al.*, 1989; Vismer *et al.*, 1996; Yassin *et al.*, 2010	
Penicillium glabrum	Okeke *et al.*, 1993	
Penicillium gladioli	Dombrinck-Kurtzman, 2007; Frisvad and Samson, 2004; Frisvad *et al.*, 2004	
Penicillium glandicola	Frisvad and Filtenborg, 1989; Houbraken *et al.*, 2016; Paterson, 2004 (IDH gene)	
Penicillium glandicola var. *glaucovenetum*	Dombrinck-Kurtzman, 2007; Frisvad and Filtenborg,1989; Paterson, 2004 (IDH gene)	see ***P. concentricum***
Penicillium granulatum	Borkowska Opacka and Escoula, 1977; Frisvad *et al.*, 1983	see ***P. glandicola***
Penicillium griseofulvum	Chunmei *et al.*, 2013; Dombrinck-Kurtzman, 2007; Dombrink-Kurtzman and Blackburn, 2005; Frisvad and Filtenborg, 1983, 1989; Frisvad *et al.*, 1987; Houbraken *et al.*, 2016; Kent and Heatley, 1945; Moslem *et al.*, 2010; Okeke *et al.*, 1993; Oh *et al.*, 1998; Paterson, 2004 (IDH gene); Simonart and Lathouwer, 1956; Steiman *et al.*, 1989; Welke *et al.*, 2011	
Penicillium griseofulvum var. *dipodomyicola*	Frisvad and Filtenborg, 1989; Frisvad *et al.*, 1987; Paterson, 2004 (IDH gene)	see ***P. dipodomyicola***
Penicillium hirsutum	Okeke at al., 1993; Paterson *et al.*, 2004	
Penicillium italicum	Okeke *et al.*, 1993	
Penicillium janczewskii	only IDH gene found, Paterson, 2004	
Penicillium lanosum	Kharchenko, 1970	
Penicillium lapidosum	Myrchink, 1967	
Penicillium leucopus	Anslow *et al.*, 1943; Brian *et al.*, 1956; Umezawa *et al.* 1947	see ***P. expansum***
Penicillium lignorum	Okeke *et al.*, 1993	
Penicillium maltum	Ukai *et al.*, 1954	see ***P. griseofulvum***
Penicillium marinum	Frisvad and Samson, 2004; Frisvad *et al.*, 2004	
Penicillium melanoconidium	Luque *et al.*, 2011	
Penicillium melinii	Frisvad and Filtenborg, 1990; Karow and Forster, 1944; Okeke *et al.*, 1993; Paterson, 2004 (IDH gene)	
Penicillium miczynskii	Chunmei *et al.*, 2013	
Penicillium novae-zeelandiae	Burton, 1949; Burton and Pausacker, 1947; Frisvad and Filtenborg, 1990	
Penicillium paneum	Boysen *et al.*, 1996; Dombrinck-Kurtzman, 2007; Frisvad and Samson, 2004; Nielsen *et al.*, 2006	
Penicillium patulum	Anslow *et al.*, 1943; Birkinshaw *et al.*, 1943; Chain *et al.*, 1942; Frisvad, 1981	see ***P. griseofulvum***
Penicillium polonicum	Luque *et al.*, 2011	
Penicillium psychrosexualis	Houbraken *et al.*, 2010	
Penicillium puberulum	El-Samawaty *et al.*, 2013; Moslem *et al.*, 2011	
Penicillium purpurogenum	Xie *et al.*, 2011	

Table 1. Continued.

Fungal species	References	Synonymised species
Penicillium raistrickii	Veselá and Veselý, 1995	
Penicillium rivolii	Berestetskii *et al.*, 1975	
Penicillium roqueforti	Bullerman, 1978; Cakmakci *et al.*, 2015; Chunmei *et al.*, 2013; Erdogan *et al.*, 2003; Leistner and Pitt, 1977; Malekinejad *et al.*, 2015; Olivigni and Steiman *et al.*, 1989; Müller and Amend, 1997; Paterson *et al.*, 2003; Vismer *et al.*, 1996	
Penicillium roqueforti chemotype II	Frisvad and Filtenborg, 1983	see ***P. paneum***
Penicillium roqueforti var. *carneum*	Frisvad and Filtenborg, 1989; Vismer *et al.,* 1996	see ***P. carneum***
Penicillium rugulosum	Leistner and Pitt, 1977; Vismer *et al.*, 1996	
Penicillium samsonianum	Houbraken *et al.*, 2016	
Penicillium sclerotigenum	Dombrinck-Kurtzman, 2007; Frisvad *et al.*, 2004	
Penicillium selandiae	*nomen nudum*, in IMI Culture Collection Catalogue, 2010; Frisvad, unpublished	see ***P. antarcticum***
Penicillium simplicissimum	Okeke *et al.*, 1993; Paterson, 2004 (IDH gene)	
Penicillium sp.	Atkinson, 1942	
Penicillium spinulosum	only IDH gene, Paterson, 2004	
Penicillium terrestre	Atkinson *et al.*, 1944	
Penicillium thomii	Borkowska Opacka and Escoula, 1977	
Penicillium urticae	Kent and Heatley, 1945; Yamamoto, 1954	see ***P. griseofulvum***
Penicillium variabile	Leistner and Pitt, 1977; Steiman *et al.*, 1989	
Penicillium verrucosum	Luque *et al.*, 2011; Moslem *et al.*, 2013; Oh *et al.*, 1998	
Penicillium viridicatum	Frank, 1972	
Penicillium vulpinum	Dombrinck-Kurtzman, 2007; Frisvad *et al.*, 2004; Houbraken *et al.*, 2016; Ismaiel and Papenbrock, 2015; Ismaiel *et al.*, 2016	
Pestalotiopsis sp.	Okeke *et al.*, 1993	
Phialophora hoffmannii	Okeke *et al.*, 1993	
Pseudodiplodia sp.	Steiman *et al.*, 1989	
Rhinocladiella atrovirens	Steiman *et al.*, 1989	
Scopulariopsis sp.	Steiman *et al.*, 1989	
Scopulariopsis flava	Okeke *et al.*, 1993	
Scytalidium lignicola	Okeke *et al.*, 1993	
Spicelleum roseum	Okeke *et al.*, 1993	
Sporormiella minimoides	Steiman *et al.*, 1989	
Sporothrix schenckii	Steiman *et al.*, 1989	
Stemphylium sp.	Okeke *et al.*, 1993	
Stemphylium vesicarium	Laidou *et al.*, 2001	
Talaromyces purpureogenus	Ismaiel *et al.*, 2016	
Talaromyces trachyspermus	Okeke *et al.*, 1993	
Trametes squalens	Steiman *et al.*, 1989	
Trichoderma pseudokoningii	Steiman *et al.*, 1989	
Trichoderma polysporum	Steiman *et al.*, 1989	
Trichophyton mentagrophytes	Steiman *et al.*, 1989	
Trichophyton persicolor	Okeke *et al.*, 1993	
Trichothecium roseum	Okeke *et al.*, 1993	
Xylaria longiana	Edwards *et al.*, 1999; Goss *et al.*, 1999; Lykakis *et al.*, 2009	

[1] Confirmed producers are in bold.

and comparison to an authentic standard (Kildgaard *et al.*, 2014). A MS/MS analysis will only yield few fragments for patulin, and thus several other verification tests have to be done to ensure that the metabolite detected is indeed patulin. In the paper by Luque *et al.* (2011) patulin was reported for several known producers and in addition species, such as *Aspergillus flavus*, *Penicillium camemberti*, and *P. verrucosum*. In tests of those fungi for patulin this has never been verified in those species (Frisvad *et al.*, 2004; Varga *et al.*, 2011b). Luque *et al.* (2011) used micellar capillary electrophoresis (retention time) and/or HPLC-MS (retention time and MS) in addition to reporting on a PCR amplicon (496 basepairs) for the FC2/IDH gene involved in the patulin biosynthesis, and despite this, they detected patulin in species that do obviously not produce patulin. Other records of patulin producers are correct, but sometimes the fungi are just synonyms of another species. An example of this is *Penicillium griseofulvum*, a very efficient and consistent producer of patulin, and three of its synonyms *P. maltum*, *P. patulum* and *P. urticae* (Pitt, 1979) have been repeatedly reported to produce patulin (Table 1).

Given the dubious accounts of patulin production by many species, a revision of confirmed and efficient producers of patulin is given in Table 1 (species in bold). Only 29 species can be reliably said to produce patulin. Among these *P. expansum* is the most important, producing patulin in apples, pears, plums and other fruits (Dombrink-Kurtzman and McGovern, 2007; Filtenborg *et al.*, 1996; Frisvad and Samson, 2004). *Penicillium sclerotigenum*, specifically associated to sweet potatoes, is also an important patulin-producing species (Yamamoto *et al.*, 1955), as is *P. griseofulvum* that may produce patulin in wheat and malted barley (Jiménez *et al.*, 1991; Ukai *et al.*, 1954; Yamamoto *et al.*, 1954). Similarly *Aspergillus clavatus* can produce patulin in malted barley (Lopez-Diaz and Flannigan, 1997). *Penicillium dipodomyicola*, another efficient patulin producer is occasionally found in foods (Dombrink-Kurtzman and McGovern, 2007; Frisvad and Samson, 2004). Members of *Penicillium* section *Roquefortorum* all produce patulin, except *P. roqueforti*. Since *P. roqueforti* is used for blue mould cheese production, it is particularly important to know whether this fungus produces this mycotoxins. The data of Nielsen *et al.* (2017) show that *P. roqueforti* has most of the gene cluster needed for production of patulin, but some genes are missing, explaining the inability of *P. roqueforti* to produce patulin. The reports of patulin production by *P. roqueforti* (Cakmakci *et al.*, 2015; Chunmei *et al.*, 2013; Erdogan *et al.*, 2003; Leistner and Pitt, 1977; Malekinejad *et al.*, 2015; Müller and Amend, 1997; Olivigni and Bullerman, 1978; Paterson *et al.*, 2003; Steiman *et al.*, 1989; Vismer *et al.*, 1996) appear to be caused by misidentifications, because the closely related species *P. carneum* and *P. paneum* both produce patulin (Boysen *et al.*, 1996). *Paecilomyces fulvus* (formerly *Byssochlamyes fulva*), *Paecilomyces niveus* (formerly *Byssochlamys nivea*) and *Paecilomyces saturatus* have all been reported to produce patulin. There has been some doubt whether *Pae. fulvus* can produce patulin (reported by Escoula, 1974; Paterson, 2004 and Sant'Ana *et al.*, 2010, but rejected by Puel *et al.*, 2007), but these species all have heat resistant ascospores (Samson *et al.*, 2009), and thus may survive in pasteurised fruit juices and produce patulin (Rice *et al.*, 1977; Sant'Ana *et al.*, 2010). *Paecilomyces niveus* and *Penicillium paneum* can grow in substrates with a high concentration of acetic acid and thus can also be found in silage, and may produce patulin there (Gallo *et al.*, 2015; O'Brien *et al.*, 2006; Scurti *et al.*, 1973). *P. antarcticum* is a marine-derived *Penicillium* species and may produce patulin on seaweed or even in shellfish (Geiger *et al.*, 2013; Vansteelandt *et al.*, 2012). *Penicillium marinum* is also marine-derived and may produce patulin in the same seaborne organisms (Frisvad and Samson, 2004).

The remaining species producing patulin are of less consequence for mycotoxin production in foods. *Penicillium gladioli* may potentially produce patulin in gladiolus bulbs, and *Penicillium glandicola* can potentially produce patulin on acorns, but flower bulbs and acorns are not used for food or feed. *Penicillium compactum*, *Penicillium novae-zeelandiae* and *Penicillium samsonianum* are soil or grass-borne fungi (Houbraken *et al.*, 2016) and *Aspergillus longivesica*, *Aspergillus giganteus*, *Penicillium clavigerum*, *Penicillium concentricum*, *Penicillium coprobium*, *Penicillium formosanum*, and *P. vulpinum* are all dung fungi and of no consequence for food safety (Frisvad and Samson, 2004).

For all of the species listed above, patulin has been detected in a large number of isolates of the producing species, for example patulin was detected in 83 out of 85 isolates of *P. expansum* by Andersen *et al.* (2004), and produced by 350/357 isolates out of *P. expansum*, by 40 out of 40 isolates in *P. griseofulvum*, by 13/13 isolates in *P. coprobium*, by 14/14 isolates in *P. glandicola*, by 14/15 strains of *P. concentricum* (= *P. glandicola* var. *glaucovenetum*), by 10/12 isolates of *P. carneum* (= *P. roqueforti* var. *carneum*), by 4/4 isolates of *P. dipodomyicola* (= *P. griseofulvum* var. *dipodomyicola*) and by 6/6 isolates of *P. vulpinum* (Frisvad and Filtenborg, 1989), showing a high consistency in patulin production by these species.

4. Penicillic acid and producing organisms

Penicillic acid is the main product of the biosynthetic pathway that starts with orsellinic acid and has penicillic acid as end product (Axberg and Gatenbeck, 1975a,b; Eldridge *et al.*, 1977). However there are other members of the penicillic acid pathway, including 5,6-dihydropenicillic acid, 5,6-dihydro-6-hydroxypenicillic acid, 6-methoxy-5,6-dihydropenicillic acid, coculnol, and (4R,5R)-4,5-

dihydroxy-3-methoxy-5-methylcyclohex-2-en-1-one (He *et al.*, 2004; Kimura *et al.*, 1996; Nonaka *et al.*, 2015; Obana *et al.*, 1995a,b; Phainuphong *et al.*, 2017; Qi *et al.*, 2015; Raphael, 1947a,b; Shiono *et al.*, 2005).

Penicillic acid has been reported in 101 species, varieties and chemotypes of fungi (Table 2), of which 48 are regarded as well documented. Some of the data may be incorrect connections between fungal species and penicillic acid because of carry over in the chromatographic system, or contamination by penicillic acid producing species. In the paper by Gutarowska *et al.* (2010), *Aspergillus niger* and *Aspergillus flavus* are reported to produce penicillic acid, and this has never been reported from these Aspergilli in any other papers. Again the isolates have not been accessioned in any fungal collection, but furthermore, the concomitant detection of penicillic acid and viridicatin indicates that the cultures of *A. flavus* and *A. niger* were contaminated with *Penicillium cyclopium*, which is a known producer of these two secondary metabolites. In the control sample on malt extract agar (MEA) with no fungi inoculated, Gutarowska *et al.* (2010) found kojic acid, indicating that a kojic acid producer had been growing in the barley malt before it was made into malt extract.

Producers of penicillic acid are especially common in *Penicillium* section *Viridicata* and in *Aspergillus* section *Circumdati* (Frisvad and Samson, 2000; Frisvad *et al.*, 2004a; Visagie *et al.*, 2014a). One can therefore expect a mycotoxin cocktail in mouldy cereals consisting of citrinin, ochratoxin A, penicillic acid, verrucosidin, nephrotoxic glycopeptides, xanthomegnin, viomellein, vioxanthin, moniliformin, and penitrem A when associated storage fungal species, such as *P. verrucosum, P. aurantiogriseum, P. polonicum, P. viridicatum, P. cyclopium* and *Penicillium freii* have grown on those cereals in a worst case scenario (Frisvad and Samson, 2004; Frisvad *et al.*, 2004; Hallas-Møller *et al.*, 2016; Lund and Frisvad, 1994). Most species in *Aspergillus* section *Circumdati*, such as *Aspergillus westerdijkiae*, *Aspergillus steynii* and *Aspergillus ochraceus* also produce one or more of the mycotoxins ochratoxin A, penicillic acid, xanthomegnin, viomellein and vioxanthin (Visagie *et al.*, 2014a). Penicillic acid has been found in many sections of *Penicillium,* including *Brevicompacta, Canescentia, Chrysogena, Exilicaulis, Fasciculata, Lanata-Divaricata, Ramosa, Roquefortorum* and *Turbatum*, so this is found in many phylogenetic groups of *Penicillium*. Penicillic acid has only been found in one section of *Aspergillus*: *Circumdati*.

Other species listed in Table 2 producing penicillic acid include soil borne species, such as *Penicillium baarnense*, *Penicillium egyptiacum*, and *Penicillium jamesonlandense*, grass-associated fungi, such as *Penicillium brasilianum* and dung fungi, such as *Penicillium bovifimosum* also produce penicillic acid, but such fungi will probably not grow in foods or feeds, and are less relevant for food safety.

Among the common species producing penicillic acid, there is a high consistency in producing this mycotoxin. In *P. aurantiogriseum*, more than 278 isolates out of 385 examined produced penicillic acid, and it was produced by 17/17 isolates of *P. melanoconidium*, by 35/53 isolates of *Penicillium neoechinulatum*, by 234/276 isolates of *P. polonicum*, and by 324/350 isolates of *P. viridicatum* (Frisvad and Filtenborg, 1989).

Terrestric acid, often co-occurring with penicillic acid, is produced by cereal borne fungi such as *P. aurantiogriseum*, *P. tricolor* and *P. hordei*, by onion and bulb associated fungi, such as *P. radicicola, P. tulipae*, and *P. venetum* in addition to being produced by the apple, cheese and nut associated *P. crustosum* and the rice associated fungus *M. grisea* (Frisvad and Samson, 2004; Yu *et al.*, 2010) (Table 3). This toxin may thus co-occur in cereals with penicillic acid, moniliformin, ochratoxin A, verrucosidins, and xanthomegnins (Frisvad and Samson, 2004).

5. Moniliformin and producing microorganisms

Moniliformin is a mycotoxin that was first reported from *Fusarium moniliforme* (Cole *et al.*, 1973), but has since been reported to be produced by many species in that genus (Table 4). It is biosynthesised from two acetyl units (Franck and Breipohl, 1984; Gathercole *et al.*, 1986). Most of the producers of moniliformin have been confirmed by data from later papers (Table 4), and rejected producers mostly are only synonyms of names later accepted. Most of these 40 species reported to produce moniliformin do indeed produce it, except for 6 species, where Schütt *et al.* (1998) could not confirm production by these species. It should be noted that moniliformin production is difficult to verify because of the low molecular weight and simple MS fragmentation pattern, so often TLC and the characteristic UV spectrum has been used to confirm identity. In the database on natural products called AntiBase, among more than 40,000 compounds, only one has a formula of $C_4H_2O_3$, so simple HR-MS data are also confirmative of production. In addition to its production by *Fusarium* species, *Penicillium melanoconidium* has been reported to produce moniliformin (Hallas-Møller *et al.*, 2016). A large number of these species are cereal-borne, including *P. melanoconidium* which has, however, only been found on stored cereals. However, other species of *Fusarium* are pathogens on potatoes, tomatoes, onions, etc. (Lesley and Summerell, 2016), and thus moniliformin can occur in many cereals, fruits and vegetables. Furthermore, moniliformin is produced by isolates of *Fusarium fusaroides* from millet, sorghum, dried fish and peanuts (Rabie *et al.*, 1978). In addition *Fusarium* species produce several other mycotoxins concomitantly, such as trichothecenes, zearalenone,

Table 2. Filamentous fungi claimed as producers of penicillic acid.[1]

Fungal species	References	Synonymised species
Aspergillus affinis	Visagie *et al.*, 2014a	
Aspergillus auricomus	Ciegler 1972; Frisvad *et al.*, 2004a; Visagie *et al.*, 2014a	
Aspergillus bridgeri	Frisvad *et al.*, 2004a; Kumar *et al.*, 2011; Visagie *et al.*, 2014a	
Aspergillus cervinus	He *et al.*, 2004	
Aspergillus cretensis	Frisvad *et al.*, 2004a; Visagie *et al.*, 2014a	
Aspergillus elegans	Obana *et al.*, 1995b	
Aspergillus flavus	Gutarowska *et al.*, 2010	
Aspergillus flocculosus	Frisvad *et al.*, 2004a; Montenegro *et al.*, 2012; Visagie *et al.*, 2014a	
Aspergillus fumigatus	Şenyuva *et al.*, 2008	
Aspergillus insulicola	Frisvad *et al.*, 2004a; Visagie *et al.*, 2014a	
Aspergillus melleus	Ciegler, 1972; Frisvad *et al.*, 2004a; Gill-Carey 1949; Obana *et al.*, 1995b; Visagie *et al.*, 2014a	
Aspergillus muricatus	Frisvad and Samson, 2000; Frisvad *et al.*, 2004a; Visagie *et al.*, 2014a	
Aspergillus neobridgeri	Frisvad *et al.*, 2004a; Visagie *et al.*, 2014a	
Aspergillus nidulans	Abu-Seidah, 2003	
Aspergillus niger	Gutarowska *et al.*, 2010	
Aspergillus occultus	Visagie *et al.*, 2014a	
Aspergillus ochraceopetaliformis	Visagie *et al.*, 2014a	
Aspergillus ochraceus	Ciegler, 1972; El-Shanawany *et al.*, 2005; Frisvad *et al.*, 2004a; Garza *et al.*, 1993; Karow *et al.,* 1944; Northolt *et al.*, 1979; Obana *et al.*, 1995b; Visagie *et al.*, 2014a	
Aspergillus ostianus	Ciegler, 1972; Frisvad *et al.*, 2004a; Namikoshi *et al.*, 2003; Obana *et al.*, 1995b; Visagie *et al.*, 2014a	
Aspergillus pallidofulvus	Visagie *et al.*, 2014a	
Aspergillus persii	Frisvad *et al.* 2004a; Visagie *et al.*, 2014a	
Aspergillus petrakii	Frisvad *et al.*, 2004a	see ***A. ochraceus***
Aspergillus pseudoelegans	Frisvad *et al.*, 2004a	
Aspergillus pulvericola	Visagie *et al.*, 2014a	
Aspergillus quercinus	Gill-Carey, 1949	
Aspergillus salwaensis	Visagie *et al.*, 2014a	
Aspergillus roseoglobulosus	Frisvad *et al.*, 2004a; Visagie *et al.*, 2014a	
Aspergillus sclerotiorum	Ciegler, 1972; Frisvad *et al.*, 2004a; Kang and Kim, 2004; Kang *et al.*, 2007; Obana *et al.*, 1995b; Visagie *et al.*, 2014a; Zheng *et al.*, 2010	
Aspergillus sp.	Li *et al.*, 2010	
Aspergillus subramanianii	Visagie *et al.*, 2014a	
Aspergillus sulphureus	Ciegler, 1972; Frisvad *et al.*, 2004a; Gill-Carey, 1949	
Aspergillus violaceus	Abu-Seidah, 2003	
Aspergillus wentii	He *et al.*, 2004	
Aspergillus westerdijkiae	Frisvad *et al.*, 2004a; Visagie *et al.*, 2014a	
Aspergillus westlandensis	Visagie *et al.*, 2014a	
Eupenicillium bovifimosum	Tuthill and Frisvad, 2002	see ***P. bovifimosum***
Exophiala sp.	Zhang *et al.*, 2008	
Malbranchea aurantiaca	Martínez-Luis *et al.*, 2005	
Paecilomyces ehrlichii	Gorbach and Friederick, 1949	
Penicillium atramentosum	Bridge *et al.*, 1989	
Penicillium aurantiogriseum	Bridge *et al.* 1989; Bokhari and Flannigan, 1996; El-Banna *et al.*, 1987; Frisvad and Filtenborg 1983; Frisvad *et al.*, 2004b; Garza *et al.*, 1993; Khaddor *et al.*, 2007; Lund and Frisvad 1994; Mills *et al.*, 1995a,b; Oh *et al.*, 1998	
Penicillium aurantiogriseum var. *polonicum*	Frisvad and Filtenborg, 1989	see ***P. polonicum***
Penicillium aurantiogriseum var. *neoechinulatum*	Frisvad *et al.*, 1987	see ***P. neoechinulatum***

Table 2. Continued.

Fungal species	References	Synonymised species
Penicillium aurantiogriseum var. *melanoconidium*	Frisvad and Filtenborg, 1989	see ***P. melanoconidium***
Penicillium aurantiovirens	Lund and Frisvad, 1994; Wirth and Klosek, 1972	presently regarded as a synonym of ***P. cyclopium***
Penicillium baarnense	Burton, 1949; Mosbach, 1960	
Penicillium bovifimosum	Tuthill and Frisvad, 2002; Visagie *et al.*, 2014b	
Penicillium brasilianum	Frisvad, 1989; Frisvad and Filtenborg, 1990 Schurman *et al.*, 2010	
Penicillium brevicompactum	Paterson *et al.*, 1987	
Penicillium canescens	Keromnes and Thouvenot, 1985; Kharchenko, 1970	
Penicillium carneum	Boysen *et al.*, 1996; Frisvad *et al.*, 2004	
Penicillium castellae	Quintanilla, 1982	see ***P. raistrickii***
Penicillium chrysogenum	Jiménez *et al.*, 1991; Leistner and Pitt, 1977; Oyero and Oyefulo, 2009	
Penicillium citrinum	Delgado *et al.*, 2011; El-Samawaty *et al.*, 2013	
Penicillium claviforme	Ueno, 1994	
Penicillium commune	Ciegler *et al.*, 1972; Mintzlaff *et al.*, 1972	
Penicillium cordubense	Skóra *et al.*, 2017	see ***P. polonicum***
Penicillium cremeogriseum	Frisvad and Filtenborg, 1990	
Penicillium cyclopium	Bentley and Keil, 1962; Birkinshaw *et al.,* 1936; Ciegler *et al.*, 1972; Frisvad and Samson, 2004; Jiménez *et al.*, 1991; Keromnes and Thouvenot, 1985; Lei *et al.*, 2010; Lindenfelser and Ciegler, 1977; Lund and Frisvad, 1994; Mintzlaff *et al.*, 1972; Northolt *et al.*, 1979	
Penicillium expansum	Ciegler *et al.*, 1972; Mintzlaff *et al.*, 1972; Patterson and Damoglou, 1985	
Penicillium fennelliae	Van Eijk, 1969	
Penicillium freii	Frisvad *et al.*, 2004; Lund and Frisvad, 1994	
Penicillium frequentans	Yamaji *et al.*, 2005	
Penicillium funiculosum	Nasser, 2008	
Penicillium granulatum	Bridge *et al.,* 1989	
Penicillium griseofulvum	Moslem *et al.*, 2010; Reio, 1958	
Penicillium griseum	Gorbach and Friederick, 1949	
Penicillium hirsutum	Bridge *et al.,* 1989; Ezzat *et al.*, 2007	
Penicillium hirsutum var. *albocoremium*	Frisvad and Filtenborg, 1989	
Penicillium islandicum	Nasser, 2008	
Penicillium jamesonlandense	Frisvad *et al.*, 2006	
Penicillium janczewskii	Frisvad and Filtenborg, 1990	
Penicillium janthinellum	Ciegler *et al.*, 1972; Mintzlaff *et al.*, 1972	
Penicillium lilacinum	Kharchenko, 1970	
Penicillium lividum	Gorbach and Friederick, 1949	
Penicillium madriti	Birkinshaw and Gowlland, 1962	also named ***P. matriti***
Penicillium martensii	Kurtzman and Ciegler, 1970; Lillehoj *et al.*, 1972; Mintzlaff *et al.*, 1972; Northolt *et al.*, 1979; Wirth *et al.*, 1956	
Penicillium megasporum	Nozawa *et al.*, 1989; not a *Penicilium* (Frisvad and Filtenborg, 1990; Visagie *et al.*, 2014b)	
Penicillium melanoconidium	Lund and Frisvad 1994; Frisvad and Samson, 2004	
Penicillium neoechinulatum	Lund and Frisvad 1994; Frisvad and Samson, 2004	
Penicillium ochraceum	Tsunoda *et al.*, 1978	see ***P. viridicatum***
Penicillium olivinoviride	Kobayashi *et al.*, 1971	see ***P. viridicatum***
Penicillium oxalicum	Oh *et al.*, 1998	

Table 2. Continued.

Fungal species	References	Synonymised species
Penicillium palitans	Ciegler and Kurtzman, 1970	
Penicillium paraherquei	Leistner and Eckardt, 1979	
Penicillium piscarium	Leistner and Pitt, 1977	
Penicillium polonicum	Frisvad and Samson, 2004; Lund and Frisvad, 1994; Skóra *et al.*, 2017	
Penicillium puberulum	Alsberg and Black 1913; El-Samawaty *et al.*, 2013; Moslem *et al.*, 2011	see ***P. cyclopium***
Penicillium pulvillorum	Frisvad and Filtenborg, 1990	
Penicillium radicicola	Frisvad and Samson, 2004; Overy and Frisvad, 2003, 2005	
Penicillium raistrickii	Bridge *et al.,* 1989; Frisvad, 1988; Frisvad and Filtenborg, 1990	
Penicillium rolfsii	Frisvad, 1989	
Penicillium roqueforti	Bridge *et al.,* 1989; Cakmakci *et al.*, 2012, 2015; Erdogan *et al.*, 2003; Moubasher *et al.,* 1978; Malekinejad *et al.*, 2015; Mioso *et al.*, 2015; Müller and Amend, 1997; Olivigni and Bullerman, 1978	
Penicillium simplicissimum	Betina *et al.*, 1969; Ciegler *et al.*, 1972; El-Banna *et al.*, 1987; Mintzlaff *et al.*, 1972; Takahashi *et al.*, 2008	
Penicillium solitum	Bridge *et al.,* 1989	
Penicillium sp.	Komagata *et al.*, 1996; Tachibana *et al.*, 2008	
Penicillium stoloniferum	Alsberg and Black, 1913; Clutterbuck *et al.*, 1932 Ciegler *et al.*, 1972; Lindenfelser and Ciegler, 1977	
Penicillium suavolens	Karow *et al.*, 1944	see ***P. carneum***
Penicillium subrubescens	Mansouri *et al.*, 2013	
Penicillium thomi/P. thomii	Karow *et al.* 1944; Casquete *et al.*, 2017	
Penicillium tulipae	Frisvad and Samson, 2004; Overy and Frisvad, 2003; Overy *et al.,* 2005;	
Penicillium vanderhammenii	Houbraken *et al.*, 2011	
Penicillium verrucosum	Gedek *et al.*, 1981; Moslem, 2013; Oh *et al.*, 1998	
Penicillium viridicatum	Bresler *et al.*, 1995; Ciegler *et al.*, 1972, 1973; Frisvad and Samson, 2004; Jiménez *et al.*, 1991; Lund and Frisvad, 1994; Mintzlaff *et al.,* 1972; Northolt *et al.*, 1979; Oh *et al.*, 1998	
Trichoderma spp.[2]	Lebed *et al.*, 1978	

[1] Confirmed producers are in bold.
[2] In this case penicillic acid is referring to a member of the penicilin biosynthetic pathway.

enniatins and several other mycotoxins or emerging mycotoxins (Brase *et al.*, 2009; Gruber-Dorninger *et al.*, 2017; Neme and Mohammed, 2017). Since moniliformin is produced by so many species one can maybe expect that apart from its mammal and plant toxicity, it could have antibiotic or quorum sensing inhibition abililites.

6. Conclusions

The small acidic lactone mycotoxins, such as patulin, penicillic acid and moniliformin can occur in many foods and feeds, and are toxic by themselves, but often there may be a potential synergistic or additive effect with other co-occurring mycotoxins. Based on the species producing patulin, fruit products are most prone to contamination with this mycotoxin. Penicillic acid is more common on stored cereals, as the best producers are mostly cereal-borne. Moniliformin is produced by a large number of *Fusarium* species, and many of those are common on cereals, but also on fruits and vegetables. Among a large number of species reported to produce patulin and penicillic acid, only 29 and 48 species, respectively, have been reliably reported to produce them. The species producing them are mostly belonging to *Penicillum* and *Aspergillus*. Moniliformin is produced by 34 *Fusarium* species and by one species of *Penicillium*. The revised lists of producers of these mycotoxins will aid in preventive mycotoxin work, but also help in de-selecting known producers of these antibiotic toxins, when screening for new antibiotics.

Table 3. Filamentous fungi reported as producers of terrestric acid.[1]

Fungal species	References	Synonymised species
Magnaporthe oryzae	Couch and Kohn, 2002 (taxonomy); Yu *et al.*, 2010	
Pyricularia oryzae	Yu *et al.*, 2010	see ***M. oryzae***
Penicillium aurantiogriseum	Frisvad and Samson, 2004; Lund and Frisvad, 1994	
Penicillium aurantiogriseum var. *aurantiogriseum*	Frisvad and Filtenborg, 1989	see ***P. aurantiogriseum***
Penicillium crustosum	Frisvad and Filtenborg, 1989; Frisvad and Samson, 2004; Sonjak *et al.*, 2005	
Penicillium griseoroseum	Da Silva *et al.*, 2013	
Penicillium hirsutum	Frisvad and Samson, 2004; Overy and Frisvad, 2003; Overy *et al.*, 2005	
Penicillium hirsutum var. *albocoremium*	Frisvad and Filtenborg, 1989	
Penicillium hirsutum var. *hirsutum*	Frisvad and Filtenborg, 1989	see ***P. hirsutum***
Penicillium hirsutum var. *hordei*	Frisvad and Filtenborg, 1989	see ***P. hordei***
Penicillium hirsutum var. venetum	Frisvad and Filtenborg, 1989	see ***P. venetum***
Penicillium hordei	Frisvad and Samson, 2004; Overy *et al.*, 2005	
Penicillium terrestre	Birkinshaw and Samant, 1960	see ***P. crustosum***
Penicillium tricolor	Frisvad and Samson, 2004; Frisvad *et al.*, 1994	
Penicillium radicicola	Overy and Frisvad, 2003; Overy *et al.*, 2005	
Penicillium tulipae	Overy and Frisvad, 2003; Overy *et al.*, 2005	
Penicillium venetum	Frisvad and Samson, 2004; Overy and Frisvad, 2003; Overy *et al.*, 2005	
Penicillium viridicatum	Birkinshaw and Samant, 1960	

[1] Confirmed producers are in bold.

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Table 4. Filamentous fungi reported as producers of moniliformin.[1]

Fungal species	References
Fusarium acuminatum	Bosch and Mirocha, 1992; Hussein *et al.*, 1991; Logrieco *et al.*, 1992; Rabie *et al.*, 1982; Schütt *et al.*, 1998
Fusarium acutatum	Schütt *et al.*, 1998
Fusarium anthophilum	Marasas *et al.*, 1986; Schütt *et al.*, 1998
Fusarium arthrosporioides	Schütt *et al.*, 1998
Fusarium avenaceum	Bosch and Mirocha, 1992; Rabie *et al.*, 1982; Schütt *et al.*, 1998
Fusarium begoniae	Fotso *et al.*, 2002; Schütt *et al.*, 1998
Fusarium beomiforme	Marasas *et al.*, 1991; Schütt *et al.*, 1998
Fusarium bulbicola	Schütt *et al.*, 1998
Fusarium chlamydosporum	Schütt *et al.*, 1998
Fusarium concentricum	Schütt *et al.*, 1998
Fusarium concolor[2]	Rabie *et al.*, 1982
Fusarium culmorum[2]	Scott *et al.*, 1987
Fusarium denticulatum	Fotso *et al.*, 2002; Schütt *et al.*, 1998
Fusarium denticulatum	Schütt *et al.*, 1998
Fusarium dlamini	Schütt *et al.*, 1998
Fusarium equiseti[2]	Bosch and Mirocha, 1992; Hussein *et al.*, 1991; Rabie *et al.*, 1982
Fusarium fujikuroi (Bakane strains)	Marasas *et al.*, 1986, 1991; Schütt *et al.*, 1998
Fusarium fusaroides	Rabie *et al.*, 1978, 1982
Fusarium lactis	Fotso *et al.*, 2002; Schütt *et al.*, 1998
(*Fusarium moniliforme*)[2]	Cole *et al.*, 1973; Burmeister *et al.*, 1979; Hussein *et al.*, 1991; Marasas *et al.*, 1986; Rabie *et al.*, 1982; Tseng, 1993
Fusarium moniliforme var. *subglutinans* (*Fusarium sacchari* var. *subglutinans*)[2] = ***Fusarium subglutinans*** (see this)	Bosch and Mirocha, 1992; Bosch *et al.*, 1992; Hussein *et al.*, 1991; Kriek *et al.*, 1977; Lew *et al.*, 1996; Logrieco *et al.*, 1993; Marasas *et al.*, 1986; Rabie *et al.*, 1982
Fusarium napiforme	Marasas *et al.*, 1991; Schütt *et al.*, 1998
Fusarium nisikadoi	Fotso *et al.*, 2002; Schütt *et al.*, 1998
Fusarium nygamai	Marasas *et al.*, 1988; 1991; Schütt *et al.*, 1998
Fusarium oxysporum	Abbas *et al.*, 1995; Hussein *et al.*, 1991; Rabie *et al.*, 1982; Schütt *et al.*, 1998
Fusarium phyllophilum	Fotso *et al.*, 2002; Schütt *et al.*, 1998
Fusarium proliferatum	Logrieco and Bottalico, 1988; Logrieco *et al.*, 1995; Marasas *et al.*, 1986; Miller *et al.*, 1995; Scarpino *et al.*, 2015; Schütt *et al.*, 1998
Fusarium pseudoanthophilum	Schütt *et al.*, 1998
Fusarium pseudocircinatum	Fotso *et al.*, 2002; Schütt *et al.*, 1998
Fusarium pseudonygamai	Fotso *et al.*, 2002; Schütt *et al.*, 1998
Fusarium ramigenum	Fotso *et al.*, 2002; Schütt *et al.*, 1998
Fusarium redolens	Schütt *et al.*, 1998
Fusarium sacchari	Schütt *et al.*, 1998
Fusarium semitectum	Rabie *et al.*, 1982;
Fusarium sporotrichioides[2]	Scott *et al.*; 1987
Fusarium subglutinans	Bosch and Mirocha, 1992; Bosch *et al.*, 1992; Hussein *et al.*, 1991; Kriek *et al.*, 1977; Marasas *et al.*, 1986; Lew *et al.*, 1996; Logrieco *et al.*, 1993; Rabie *et al.*, 1982; Schütt *et al.*, 1998
Fusarium temperatum	Scauflaire *et al.*, 2011; Sewram *et al.*, 1999
Fusarium thapsinum	Schütt *et al.*, 1998
Fusarium tricinctum	Schütt *et al.*, 1998
Penicillium melanoconidium	Hallas-Møller *et al.*, 2016

[1] Confirmed producers are in bold.
[2] Not confirmed by Schütt *et al.* (1998), regarded here as the authoritative statement regarding taxonomy of the Fusaria.

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